

PREDATORY BEHAVIOUR IN THE ANT-LIKE WASP *METHOCHA STYGIA*
(SAY) (HYMENOPTERA: TIPHIIDAE)

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Abstract. An examination of prey-orienting behaviour of *Methocha stygia* has demonstrated that adult females regularly transport prey (*Cicindela* larvae) when they are removed from their burrows. On a single occasion a wasp was also observed to utilize a naturally occurring depression in the soil as a nest site, instead of depending on the prey's own burrow. This flexibility in response might be a carry-over of the behaviour that surely existed in the ancestors of the methochine wasps, insects which were close to if not identical with the ancestors of the ants. When *Methocha* females were crowded together with prey in the laboratory, frequent avoidance and aggressive behaviours were noted, but no sign of any form of co-operation.

The Tiphiidae are a rather diverse family of wasps consisting of six subfamilies, most of which are not extensive in the North American fauna. The Methochinae, for example, are represented by only five species, two on the west coast, two on the east coast and one, *Methocha stygia*, ranging broadly over the United States and southern Canada (Muesebeck, Krombein & Townes 1951).

The biology of the Methochinae is not well known, since they are rather rare or local insects, but it is clear that those species which have been studied all exhibit strong sexual dimorphism, the female being apterous and smaller than the winged male. All are parasitoids of tiger beetle (*Cicindelidae*) larvae. The attack behaviour of *M. stygia* was studied briefly by Williams (1916); more recently, Burdick & Wasbauer (1959) examined various aspects of the biology of *M. californica*, with special reference to predatory behaviour. It seems clear that the female is morphologically and behaviourally specialized to allow itself to be seized by the cicindelid larvae without harm. The wasp positions itself in such a manner that the jaws of the beetle encircle the narrow thorax or petiole waist of the wasp but cannot crush it. As the beetle larva rears upward to seize its would-be victim, it exposes its lightly chitinated neck which the wasp quickly stings. Further stinging takes place and the wasp drags the beetle to the bottom of the burrow, lays a single egg on it, and then carefully fills the burrow up by transporting bits of soil into it.

Because of their largely generalized morphology and primitive behaviour, the Scolioidea, to which the Tiphiidae belong, are generally regarded as the most primitive extant superfamily of aculeate Hymenoptera. Moreover, because of an almost total absence of pre-Tertiary aculeate fossil material, and with no evidence to the contrary, the Scolioidea, or their immediate progenitors, are regarded as the most likely ancestors of the other aculeate superfamilies (Evans 1958).

Recently, Wilson, Carpenter & Brown (1967) described a fossil aculeate dating from the middle of the Cretaceous period. Although the species, *Sphecomyrma freyi*, was placed in its own subfamily, it was easily recognizable as an ant. At the same time, it possesses a mosaic of wasp-like and ant-like character states. With the aid of H. E. Evans, Wilson and his co-authors made an external morphological comparison between the fossil and a number of species of modern aculeates from nine families, including the ants themselves. Although, in balance, the fossil resembled the modern ants more closely than any other aculeate family, a strong resemblance to living species of *Methocha* was also apparent.

Wilson et al. (1967) pointed out the dangers of concluding a relationship between the Methochinae and the ants, especially since the Methochinae have been evolving for at least the 100 million years since the time *S. freyi* was fossilized. It is certainly conceivable that some of the morphological similarities between the fossil and *Methocha* are the result of convergent evolution. It is also clear that the Methochinae have become highly specialized as parasitoids of cicindelid larvae. However, it would still be of

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considerable interest to learn the full range of behavioural responses of *Methocha*, in both natural and stressed circumstances. Specifically, the question needs to be answered: Is there any indication that *Methocha* still retains certain behavioural characters of the type which would have existed in the presumptive common ancestor of the ants and the modern *Methochinae*?

Methods

Approximately twenty females of *Methocha stygia* were studied and subsequently captured in a sandy area of about 1.2 ha at the edge of a woods in Littleton, Massachusetts. Tiger beetle larvae (*Cicindela* sp.) were abundant in the area, and a number were also captured and returned to the laboratory.

Two rather different observational procedures were undertaken in the laboratory. In one, a polystyrene container, approximately $30 \times 20 \times 10$ -cm deep, was filled with moist sand to depths ranging from 3 to 6 cm and several *Cicindela* larvae turned loose and allowed to dig burrows. Subsequently varying numbers of *Methocha* females were placed in the container, and their behaviour observed.

The second procedure involved a $25 \times 15 \times 2$ -cm wide container, placed on edge and virtually filled with moist sand, to which five *Cicindela* larvae were added in sequence. Before the beetle larvae could excavate new burrows, *Methocha* females were added one by one, and the resulting interactions observed and recorded.

Results

In the first observation chamber, it was immediately apparent that the *Methocha* females were very adept at finding and stinging the *Cicindela* larvae without harm to themselves. When the wasps entered their burrows, the larvae usually flipped out of their burrows by a violent twisting motion of their bodies. This response is obviously adaptive under natural conditions, since larvae were several times seen to escape wasps in the field as a direct result. However, under crowded experimental conditions the larvae were frequently caught and stung on the surface of the sand. Often the wasps then dragged the *Cicindela* back to their own newly abandoned burrows, providing these were no more than several centimetres from the point of capture. On other occasions, the wasps soon lost interest and abandoned the larvae, which were then typically found and stung by other wasps. Since

the wasps routinely fed upon the haemolymph escaping from the point of entrance of the sting, a number of the larvae soon expired on the surface of the sand, appearing largely drained of fluid.

On one occasion, a larva flipped out of its burrow and chanced to land in a slight depression in the sand in a corner of the container, whereupon it was soon discovered and stung by another wasp. On this occasion, the wasp made no attempt to drag the beetle back to its burrow, but instead buried it on the spot by excavating and transporting clusters of sand grains with its mandibles.

The other observation chamber, being very narrow, afforded ample opportunity for observing the nature of the interaction and activities within the beetle burrow. In one instance, a beetle which flipped out as the wasp was entering its burrow travelled 10 cm through the air. Subsequently, contact was re-established as the larva crawled over the sand, and the wasp stung the larva when it was only 1 cm from its burrow. As it dragged the larvae into the burrow the prey chanced to go in head first. Evidently this was an unsuitable orientation, for the wasp laboured for 20 min to align the larva in a head-up position but to no avail. Finally, it abandoned the larva, which appeared fully recovered some 6 hr later.

In two other instances, the larva was unable to escape and was stung, dragged to the bottom of the burrow which the wasp enlarged somewhat, allowing the larva to assume a sigmoid configuration. The wasp then laid an egg on the larva, emerged to the outside, and proceeded to transport sand grains to the burrow until the space above the larva's body was filled. This sequence of behaviour is essentially the same as that reported by Williams (1916) for *Methocha stygia* and by Burdick & Wasbauer (1959) for *Methocha californica*.

In yet another case, a larva flipped out as it was being stung, and it chanced to land, in a paralysed state, less than 2 cm from the burrow of another beetle. The wasp wandered about for a moment, apparently confused, then invaded the second burrow, whose occupant also flipped out, evidently just as it was being stung, and landed at the side of the first larva. The wasp antennated both larvae, then examined both burrows, and finally grasped the first larva, dragged it directly over the entrance of the burrow of the second larva and returned to its original burrow where it repeatedly stung the

larva, laid a single egg, and covered the larva within the burrow. This single observation suggests, but is not sufficient to prove, that *Methocha* females are able to recognize the burrows of individual prey.

Because the *Methocha* and *Cicindela* were in artificially dense concentrations in the laboratory cages (there was one *Cicindela* larva per 60 cm², or roughly ten times the concentration in the field), contacts among the hunting wasps were frequent. Usually the response was a simple avoidance: a quick turning away and departure. Wasps already in possession of a larva were often left alone without being challenged. However, in other instances the wasps fought for possession of the same larva, most often by tug-of-war. In a few cases competition for a larva led to aggression: one *Methocha* seized another by the petiole and attempted to pull it backward. We observed one chain of three *Methocha*, one tugging at the 'lead' wasp while being pulled itself by another wasp standing behind it. No sign of co-operation was observed among the wasps in hunting, killing, transporting, or burying, even though the opportunities to do so were frequent.

Discussion

Evans (1958), elaborating an earlier theoretical scheme by W. M. Wheeler, arrayed the various species of aculeate wasps along a series of thirteen evolutionary steps from a very elementary, non-social form of behaviour (egg laid on prey wherever the prey happens to be) through steps of increasing degrees of parental care and finally to a fully eusocial state with morphologically distinguishable castes, as epitomized by the hornets and wasps of the subfamily Vespinae. Since the evolution toward social behaviour has been so frequent in the aculeate Hymenoptera, arising separately within the Formicoidea, Vespoidea, and Pompiloidea-Sphecoidea-Apoidea lineages, it is obviously of considerable interest to consider the precursors of this behaviour in more primitive aculeate stocks.

Evans (1958) aptly spoke of the evolutionary transition from the habit of simply laying the egg where the prey happens to be found to a movement of the prey into a suitable niche and finally into a prepared nest as 'the very first step in the direction of the family association which we speak of as an insect society.' The majority of the Scolioidea, excluding only some Scoliidae, have not achieved this first step. Studies by earlier authors suggested that *Methocha* has

not taken this first step either. It is, therefore, of considerable interest to note that at least under laboratory conditions *M. stygia* regularly transports prey that initially escaped from their burrows before being captured. Also, one of our female *Methocha* demonstrated sufficiently plastic behaviour to take advantage of a naturally-occurring depression in the substrate as a substitute nest for the beetle larva's own burrow. In other words, *M. stygia* is capable, under the right conditions, of behaviour that places it one step closer to the ants than the great majority of other scolioid wasps.

The transport behaviour described seems to be a counter-adaptation to the prey's tendency to slip out of the burrow. It greatly increases the likelihood of proper utilization of the stung larva. An alternative adaptation would have been for the wasp simply to dig a new nest at the site of capture of the prey. Such an adaptation, of course, would represent the first small step towards sociality. There are indications that both adaptations exist in *M. stygia*, although it would seem that in the majority of cases the larvae are returned to their own burrows. It is apparent that the ancestors of the ants emphasized the second alternative. The existence of both responses in modern *M. stygia*, however, might be interpreted as indicating retention of a behaviour seen in its own ancestor as well as in the ancestor of the ants. There is no indication on the basis of these results, therefore, that the two ancestors could not, in fact, have been the same.

Another finding of potential evolutionary interest is the total absence of co-operative behaviour among the female wasps, even when the opportunities were enhanced by crowding in the laboratory environment. This negative result is consistent with the generally accepted view that social life in the ancestors of modern ants arose by greater cohesiveness of family groups, as opposed to the association of unrelated adults of the same generation (Wilson 1971).

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